

OSTEOLOGICAL DEVELOPMENT OF THE CHANNICHTHYIDAE (TELEOSTEI: NOTOTHENIOIDEI)*

by

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ABSTRACT. - The osteological development of eight species (*Champscephalus gunnari* Loennberg 1905, *Channichthys rhinoceros* Richardson 1844, *Pseudochaenichthys georgianus* Norman 1937, *Pagetopsis macropterus* (Boulenger 1907), *Chionodraco rastrispinosus* DeWitt & Hureau 1979, *Chaenodraco wilsoni* Regan 1914, *Chaenocephalus aceratus* (Loennberg 1906) and *Cryodraco antarcticus* Dollo 1900) of the most advanced among the notothenioid family Channichthyidae was examined. All the studied channichthyids in general show a sequence in the formation of bones similar to the sequence found in the most advanced nototheniids (*Pleuragramma antarcticum* (Boulenger)) and bathydraconids (*Parachaenichthys*). Morphogenesis of the skeleton of the channichthyids is the slowest one within all the notothenioids, that is probably the manifestation of a paedomorph evolution of the suborder Notothenioidei. Within channichthyids, the rate of the osteological development also becomes slower along the line *Champscephalus-Pseudochaenichthys-Pagetopsis-Channichthys-Chionodraco-Chaenodraco-Chaenocephalus-Cryodraco* that supports the point of view of Iwami (1994) on the role of paedomorphosis in speciation of the channichthyids.

RÉSUMÉ. - Développement ostéologique des Channichthyidae (Teleostei: Notothenioidei).

Nous avons étudié le développement ostéologique de huit espèces de la famille des Channichthyidae (*Champscephalus gunnari* Loennberg 1905, *Channichthys rhinoceros* Richardson 1844, *Pseudochaenichthys georgianus* Norman 1937, *Pagetopsis macropterus* (Boulenger 1907), *Chionodraco rastrispinosus* DeWitt & Hureau 1979, *Chaenodraco wilsoni* Regan 1914, *Chaenocephalus aceratus* (Loennberg 1906) et *Cryodraco antarcticus* Dollo 1900), la famille la plus évoluée des Notothenioidei. Toutes ces espèces de Channichthyidae montrent une succession dans la formation des os semblable à celle des Nototheniidae (*Pleuragramma antarcticum* (Boulenger)) et Bathydraconidae (*Parachaenichthys*). La morphogénèse des différentes parties du squelette des Channichthyidae est plus ou moins uniforme aux stades précoces du développement. La formation du squelette osseux des Channichthyidae est plus lente que celle des autres Notothenioidei, ce qui est peut-être lié à l'évolution pédomorphique du sous-ordre des Notothenioidei. Au sein même des Channichthyidae, le développement du squelette osseux se ralentit selon la succession suivante: *Champscephalus-Pseudochaenichthys-Pagetopsis-Channichthys-Chionodraco-Chaenodraco-Chaenocephalus-Cryodraco*. Ainsi le point de vue d'Iwami (1994) à propos du rôle de la pédomorphose dans la formation des espèces de Channichthyidae se confirme.

Key-words. - Notothenioidei, Channichthyidae, PS, Antarctic Ocean, Osteological development, Paedomorph evolution.

The family Channichthyidae is the most advanced among the fishes of the suborder Notothenioidei (Iwami, 1985; Balushkin, 1992; Eastman, 1993). The channichthyids

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are characterized by such peculiarities as a considerable reduction of the bony skeleton and specific structure of seismosensory system (Iwami, 1985), a reduction of erythrocytes number (Hureau, 1966; Spillmann and Hureau, 1967) and a loose of hemoglobin (Ruud, 1954). It is interesting to discover which ontogenesis process could be related to the origin of those characters of the channichthyids. For this purpose the osteological development of eight species of channichthyids was investigated. A comparative analysis was made on the sequence of appearance, morphogenesis and rate of development of various elements of the bony skeleton of channichthyids, nototheniids and bathydraconids.

MATERIAL, METHODS AND TERMINOLOGY

The material used for this study belongs to the collections of antarctic fishes of the Alfred Wegener Institute for Polar and Marine Research (Germany) collected by A. Kellermann and W. Ekau, of the Biological Station of Gdansk University (Poland) collected by W. Słozarczyk and K. Skora and of the Zoological Institute of the Russian Academy of Sciences collected by A.F. Pushkin. Altogether about 120 specimens of 8 species of channichthyids (*Champsocephalus gunnari* Loennberg 1905, *Channichthys rhinocerus* Richardson 1844, *Pseudochaenichthys georgianus* Norman 1937, *Pagetopsis macropterus* (Boulenger 1907), *Chionodraco rastrospinosus* DeWitt and Hureau 1979, *Chaenodraco wilsoni* Regan 1914, *Chaenocephalus aceratus* (Loennberg 1906) and *Cryodraco antarcticus* Dollo 1900) were studied using the method of Potthoff (1984). Since I do not have day-to-day series, I referred to the standard length to identify the ontogenetic stages. Drawings were made with a drawing tube fixed to a stereo-microscope. For the skull and pectoral girdle, the currently used terminology of Harrington (1955) and Jollie (1986) was followed; for the axial and caudal skeleton, the terminology of Monod (1968) was adapted.

RESULTS

Sequence of appearance

All the studied species of channichthyids in general show the same sequence of appearance of the different bones during ontogenesis (Table I). Among other notothenioids some similar sequence of appearance of bony elements was previously found in the nototheniid *Pleuragramma antarcticum* (Voskoboinikova, 1994; Voskoboinikova *et al.*, 1994) and in the bathydraconid *Parachaenichthys* which are the most advanced taxa into these families. Heterochronies between the studied channichthyids and *Parachaenichthys* are revealed in a later appearance of the bones of the hyoid arch, some bones of the neurocranium such as the supraoccipital, sphenoticum, prooticum, parietal, lateral ethmoid and mesethmoid. The teeth, infraorbitals, bones of the suspensorium, basi- and exoccipitals, vomer appear earlier in the channichthyids. In comparison with *Pleuragramma* it was found a later appearance of the bones of hyoid and gill arches and an earlier appearance of the teeth, interorbitals, mesopterygoid and palatine.

Probably, late appearance of some bones in the channichthyids is related with their reduction in adults. So, the bones of the ethmoidal region are very small in adult channichthyids (Iwami, 1985) where they lost their supporting function of the upper jaw and palatine. It is possible to suggest that the reduction of the mesethmoid led to the

Table I. - The appearance of bones in the ontogeny of the Channichthyidae (expressed in standard length of the larvae). 1: *Champscephalus gunnari*; 2: *Pseudochaenichthys georgianus*; 3: *Pagetopsis macropterus*; 4: *Channichthys rhinoceros*; 5: *Chionodraco rastrispinosus*; 6: *Chaenodraco wilsoni*; 7: *Chaenocephalus aceratus*; 8: *Cryodraco antarcticus*.

Bones	Species							
	1	2	3	4	5	6	7	8
	Number of specimens							
	17	19	4	10	21	13	16	14
Mesethmoid	48.5	34.0	-	39.0	40.0	35.0	64.2	70.0
Lateral ethmoid	105.0	81.0	-	-	-	61.0	86.0	-
Frontal	22.3	27.0	19.0	18.5	20.0	27.0	35.0	27.0
Nasal	29.2	22.0	31.5	14.0	34.0	37.5	34.0	70.0
Parietal	48.5	34.0	31.5	32.2	45.0	52.0	62.0	78.0
Vomer	28.0	32.0	31.5	39.0	39.0	43.0	34.0	82.0
Parasphenoid	16.5	22.0	17.5	18.5	20.0	27.0	21.0	27.0
Pterosphenoid	105.0	81.0	-	54.7	61.0	58.0	73.0	102.2
Prootic	48.5	36.0	-	39.0	58.0	58.0	64.2	102.2
Sphenotic	48.5	36.0	31.5	32.2	45.0	35.0	34.0	58.5
Pterotic	27.0	25.0	31.5	20.0	34.0	37.5	34.0	49.0
Epiotic	48.5	42.5	-	35.0	45.0	43.0	62.0	78.0
Intercalar	63.0	36.0	-	54.7	61.0	-	64.2	102.2
Post-temporal	24.5	27.0	31.5	20.0	35.0	37.5	30.5	32.0
Supraoccipital	48.5	36.0	39.0	35.0	49.0	43.0	62.0	78.0
Exoccipital	29.2	34.0	31.5	32.2	39.0	37.5	56.5	49.0
Basioccipital	27.0	27.0	31.5	20.0	27.0	27.0	34.5	44.0
Maxillae	16.5	22.0	17.5	18.5	20.0	27.0	21.0	27.0
Premaxillae	16.5	22.0	17.5	18.5	20.0	27.0	21.0	27.0
Dentary	16.5	22.0	17.5	18.5	20.0	27.0	21.0	27.0
Anguloarticular	16.5	22.0	17.5	18.5	20.0	27.0	21.0	27.0
Retroarticular	18.7	22.0	17.5	18.5	20.0	27.0	21.0	27.0
Palatine	29.2	36.0	-	47.2	49.0	52.0	62.0	70.0
Quadrate	18.7	22.0	-	18.5	20.0	27.0	30.5	27.0
Mesopterygoid	24.5	22.0	31.5	32.5	39.0	36.0	34.0	49.0
Metapterygoid	28.0	36.0	39.0	32.5	43.0	39.0	56.5	70.0
Hyomandibular	29.2	32.0	39.0	32.5	45.0	39.0	56.5	70.0
Symplectic	28.5	22.0	31.5	32.5	34.0	27.0	34.0	70.0
Interhyal	48.5	32.0	-	35.0	49.0	43.0	64.2	102.2
Epihyal	29.2	27.0	-	32.2	45.0	39.0	56.5	82.0
Ceratohyal	24.5	22.0	31.5	24.0	39.0	27.0	42.0	49.0
Lower hypohyal	36.0	36.0	-	35.0	45.0	43.0	45.0	70.0
Basihyal	48.5	45.0	-	39.0	75.0	58.0	64.2	102.2
Urohyal	36.0	36.0	-	35.0	50.0	48.0	64.2	102.2
Hypobranchial 1	48.5	45.0	-	39.0	58.0	60.0	64.2	102.2
2	48.5	45.0	-	47.2	61.0	65.0	64.2	-
3	61.0	45.0	-	47.2	75.0	-	73.0	-
Ceratobranchials 1-5	24.5	27.0	31.5	37.0	29.0	27.0	30.5	27.0
Epibranchials 1-4	48.5	42.5	-	39.0	55.0	58.0	64.2	102.2
Pharyngobranchials 2,3	27.0	27.0	31.5	29.0	29.0	39.0	21.0	27.0
Opercle	16.5	25.0	17.5	18.5	20.0	27.0	30.5	27.0
Preopercle	22.3	25.0	19.0	18.5	20.0	27.0	30.5	29.5

Table I - Continued.

Bones	Species							
	1	2	3	4	5	6	7	8
	Number of specimens							
	17	19	4	10	21	13	16	14
Interopercle	24.5	27.0	31.5	20.0	27.0	27.0	30.5	32.0
Subopercle	24.5	25.0	19.0	18.5	27.0	27.0	30.5	32.0
Lacrima	22.3	22.0	31.5	18.5	27.0	35.0	30.5	29.5
Dermosphenotic	48.5	42.5	31.5	39.0	50.0	58.0	64.2	102.2
Infraorbitals 2	28.5	36.0	-	47.2	58.0	61.0	62.0	102.2
3	48.5	36.0	31.5	35.0	50.0	62.0	62.0	102.2
4	28.5	22.0	31.5	32.2	34.0	43.0	34.0	78.0
5	48.5	36.0	31.5	35.0	59.0	52.0	56.5	78.0
6	48.5	36.0	31.5	35.0	59.0	52.0	56.5	78.0
7(8)	48.5	-	-	-	-	-	-	-
Cleithrum	16.5	27.0	17.5	18.5	20.0	27.0	21.0	27.0
Coracoid	48.5	36.0	-	39.0	55.0	48.0	62.0	78.0
Scapula	48.5	34.0	39.0	39.0	49.0	43.0	62.0	70.0
Radials 2	48.5	34.0	-	39.0	45.0	43.0	62.0	70.0
3	29.2	34.5	31.5	32.2	45.0	43.0	56.5	70.0
4	29.2	34.0	31.5	32.2	45.0	39.0	56.5	70.0
5	48.5	40.0	-	39.0	52.0	48.0	62.0	78.0
Supracleithrum	21.7	27.0	31.5	18.5	35.0	37.5	30.5	32.0
Urostyle	27.0	32.0	31.5	32.2	39.0	37.5	34.0	44.0
Hypurals 1+2	27.0	32.0	31.5	32.2	34.0	39.0	34.0	63.5
3	27.0	32.0	31.5	37.0	34.0	39.0	37.0	63.5
4	29.2	34.0	-	37.0	34.0	39.0	37.0	63.5
3+4	48.5	47.0	-	47.2	43.0	43.0	37.0	78.0
Parhypural	27.0	36.0	31.5	32.2	49.0	43.0	37.0	63.5
Epurals 1,2	48.5	50.0	39.0	47.2	75.0	65.0	64.2	102.2
3	56.5	52.0	-	54.7	75.0	-	73.0	-

formation of the rostral spine of this bone. The rostral spine has different sizes and orientations but no obvious functional utility in many species of channichthyids. The bones of hyoid and gill arches and also singulars in the channichthyids have also lost their main function of creating a negative pressure during breathing and catching the food. It is well known that oxygen exchange in this family is carried out by the capillary net of the skin and that gills do not actively participate in respiration. Moreover, the channichthyids are carnivorous and catch their prey with their long jaws supporting strong teeth. Possibly, decreasing of the role of the opercular bones in respiration and feeding led to their reduction together with the appearance of numerous spines on the opercle, sub- and interopercles (*Channichthys*, *Chionodraco*, *Chaenodraco*). Iwami (1994) proposed that the structure of the singulars of the channichthyids is a result of heterochrony, but as a difference from the bones of hyoid and gill arches there is no obvious heterochrony in the appearance of opercular bones among the studied notothenioids.

On the contrary, the earlier appearance of some bony elements is probably related to increasing of their functions and/or complication of their structure. So, earlier appearance

rance of the infraorbitals in the channichthyids is probably related to their complex structure compared to most of the other notothenioids (Iwami, 1985). As our study shows, the increase of the number of infraorbitals is mainly due to multiplication of the infraorbital 4 of the nototheniids and bathydraconids. The infraorbital 2 which is enlarged in adults of *Pseudochaenichthys*, *Pagetopsis* and *Neopagetopsis* appears later in all the genera of channichthyids and its unusual structure in above mentioned three genera is a result of a later development. It was noted that larvae of the channichthyids have well developed jaws and teeth already at the early stages of development after hatching and they become carnivorous very early (North, 1990; North and Kellermann, 1990). Adult channichthyids have very long and strong jaws with strong teeth. Obviously, the lengthening of the lower jaw has made necessary the reinforcement of supporting bony elements. In particular, it concerns the structure of anterior part of the suspensorium. It was shown a reduction of the pterygoid bones and palatine in the notothenioids (Voskoboinikova, 1982). In the nototheniids and also bathydraconids, these bones really appear later than the other elements of the suspensorium. But in the channichthyids the role of these elements increases, e.g. the mesopterygoid and palatine, which appear earlier, attain a greater development and quite another structure (Voskoboinikova, 1982; Iwami, 1985). Possibly the full reduction of the ectopterygoid promotes a better development of the mesopterygoid. It is interesting to note that the similar structure in the bathydraconids *Gerlachea* and *Parachaenichthys* origins on account of the ectopterygoid while the mesopterygoid is quite reduced. In the channichthyids two separate parts of the palatine appear and later fuse between each other. Because of that fusion, Iwami (1985) considered the possibility that the ventral part of the palatine was made of the mesopterygoid. But it is clear from the figure 2 (B, C) that the mesopterygoid appears in the channichthyids at the usual place for the notothenioids. Moreover, the ventral part of the palatine cannot be the ectopterygoid because it appears above the mesopterygoid and does not appear under this bone as usually the ectopterygoid does.

Morphogenesis

All the studied channichthyids are characterized by a rather similar development of the shape of the neurocranium, splanchnocranium, pectoral girdle and axial skeleton. At the early stages the neurocranium has a relatively compact shape with enough broad interorbital space, a more or less long ethmoidal region and a rather high skull (Fig. 1A). In general at that stages the structure of the neurocranium of the channichthyids is very similar to the structure of the nototheniids and bathydraconids differing only by the length of the ethmoidal region. With growth of larvae, the width of the interorbital space and length of the ethmoidal region increase, and the height of the skull decreases (Fig. 1B, C). Among the channichthyids, *Cryodraco* has the longest ethmoidal region. In young larvae of the channichthyids, the structure of the splanchnocranium is also very similar to the structure of the bathydraconids. The heads of the quadrate and the antero-dorsal process of the hyomandibular lie along the same vertical line (Fig. 2A): this is different from the nototheniids where the heads of the quadrate are situated much more anteriorly. Later, the anterior dorsal process of the hyomandibular moves slightly posteriorly (Fig. 2B, C). The posterior process of the quadrate is relatively short, both in larvae and adult fish, that is a difference with the nototheniids. At the early stages, the channichthyids have a rather high splanchnocranium which is conserved in the adults. Marked differences in the structure of the splanchnocranium between nototheniids and channichthyids are probably related to the great lengthening of the lower jaw in the channichthyids and the necessity to create a significant power for closing the mouth.

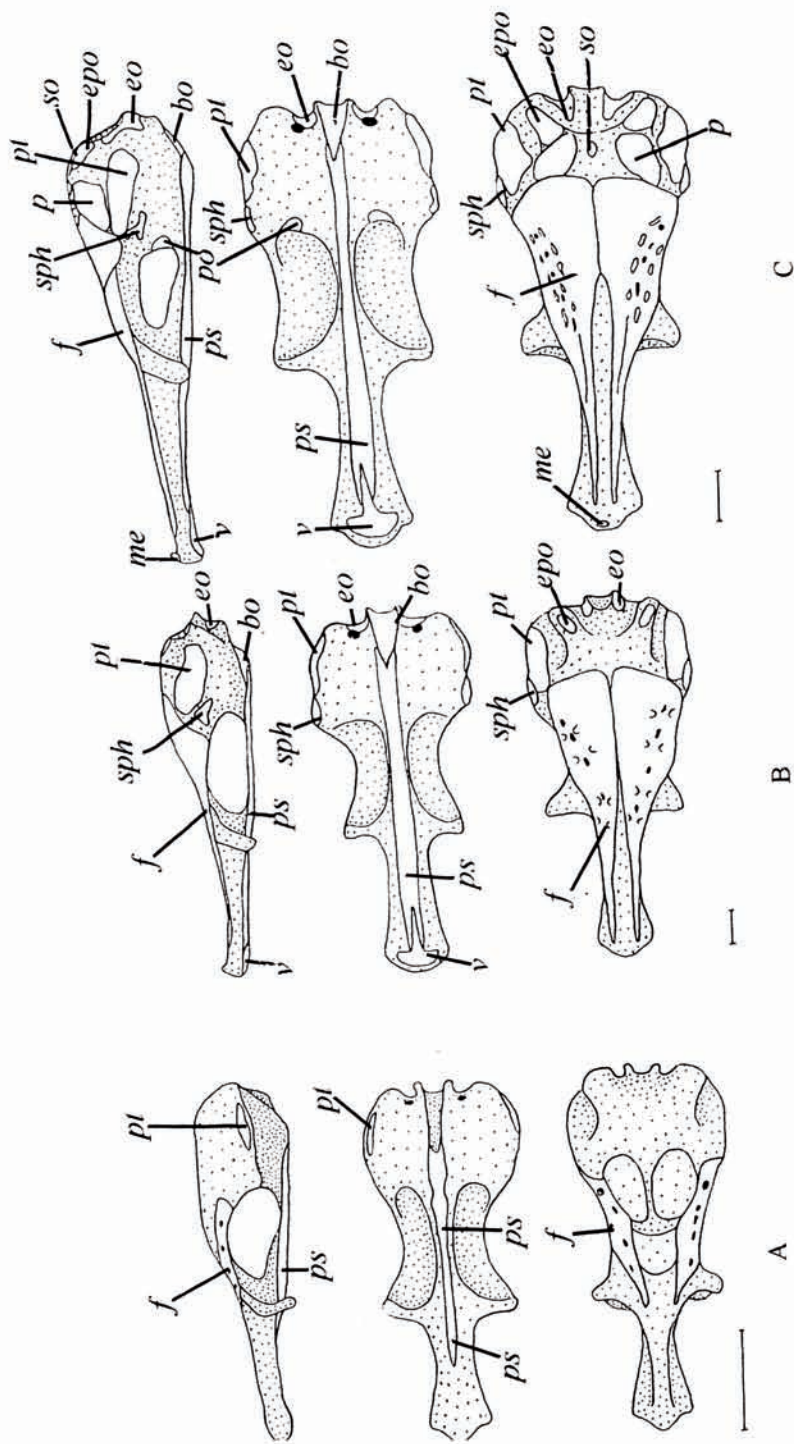


Fig. 1. - Development of the neurocranium of *Pseudochuachichthys georgianus*, showing dorsal, ventral and left lateral views. Standard lengths: (A) 27.0 mm; (B) 43.0 mm; (C) 47.0 mm. Scale bar = 1 mm. Cartilage is stippled, ossifying bones are white. Abbreviations: *bo*: basioccipital; *eo*: exoccipital; *epo*: epiotic; *f*: frontal; *me*: mesethmoid; *p*: parietal; *po*: prootic; *ps*: parasphenoid; *pt*: pterotic; *psph*: pterosphenic; *sph*: sphenoid; *sph*: supraoccipital; *v*: vomer.

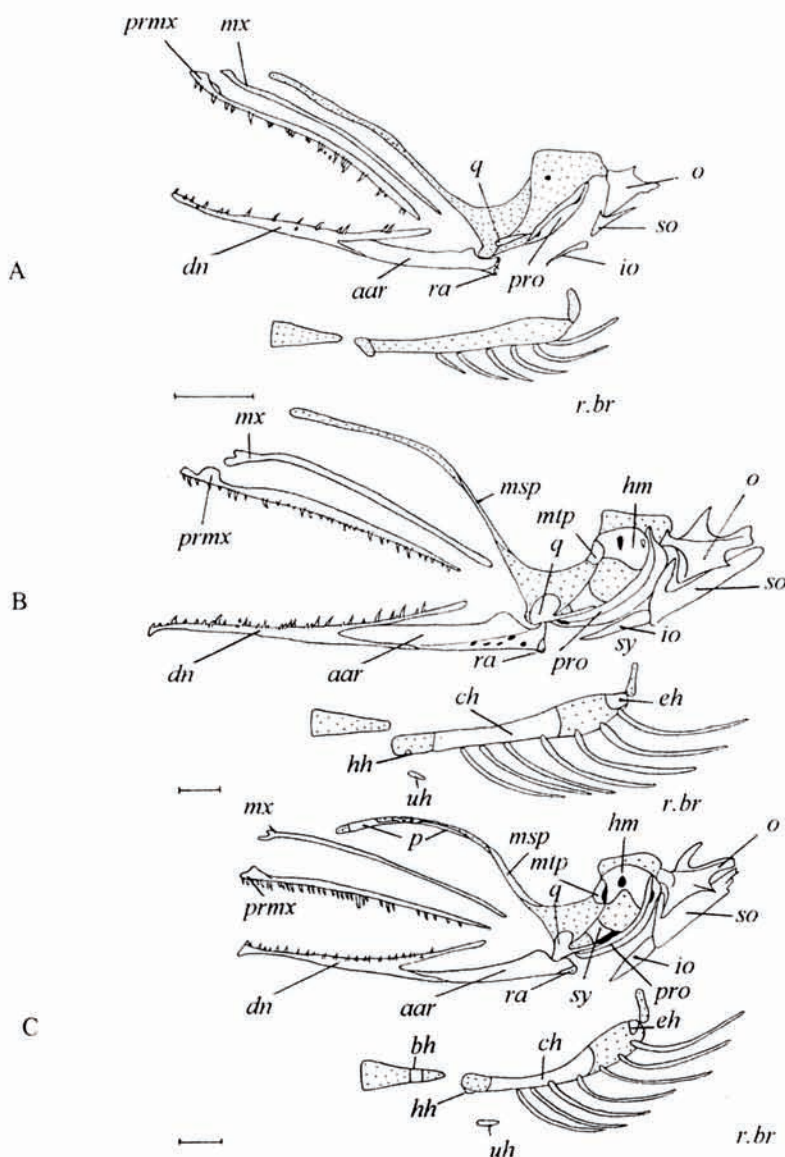


Fig. 2. - Development of the splanchnocranium of *Pseudochaenichthys georgianus*. Standard lengths: (A) 22.0 mm; (B) 40.0 mm; (C) 47.0 mm. Scale bar = 1 mm. Abbreviations: aar: anguloarticular; bh: basi-hyal; ch: ceratohyal; dn: dentary; eh: epihyal; hh: hypohyal; hm: hyomandibular; io: interopercle; msp: mesopterygoid; mtp: metapterygoid; mx: maxilla; o: opercle; p: palatine; prmx: premaxilla; pro: preopercle; q: quadrate; ra: retroarticular; r.br: branchiostegal rays; so: subopercle; sy: symplectic; ur: urohyal.

From the early stages to adults all the channichthyids are characterized by the presence of long and weak hyoid and gill arches (Fig. 2A-C).

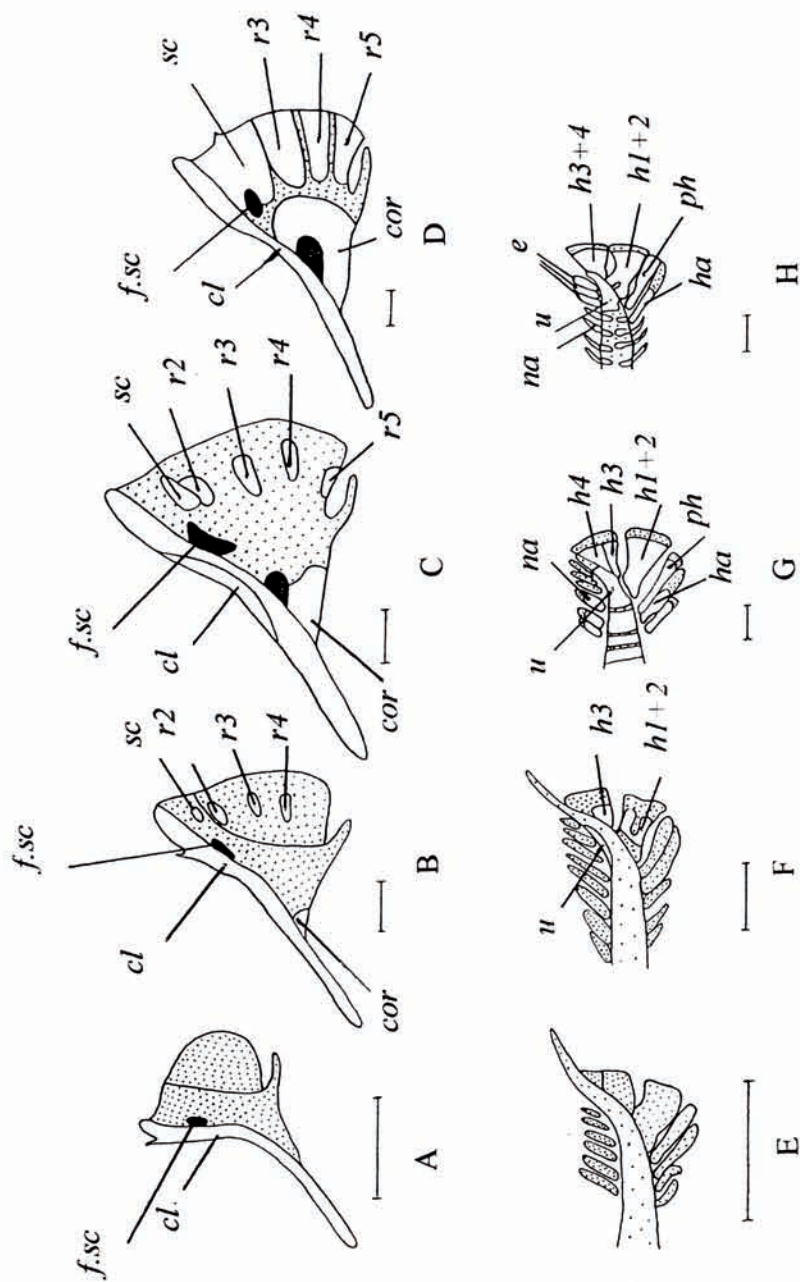


Fig. 3. - Development of the pectoral girdle, pectoral radials and caudal skeleton of *Pseudochuenichthys georgianus* (A, B, C), *Chionodraco rastrispinosus* (D, F, G) and *Chaenoecephalus aceratus* (E, H). Standard lengths: (A) 22.0 mm; (B) 27.0 mm; (C) 47.0 mm; (D) 61.0 mm; (E) 35.0 mm; (F) 39.0 mm; (G) 61.0 mm; (H) 62.0 mm. Scale bar = 1 mm. Abbreviations: cl: cleithrum; cor: coracoid; e: epurals; f.sc: scapular foramen; ha: haenal arch; h: hypural; na: neural arch; ph: parhypural; r: radial; sc: scapula; ur: urostyle.

At the early stages of all the species, a remnant of the pharyngobranchial 4 with one tooth is found; it will later fuse together with the pharyngobranchial 3.

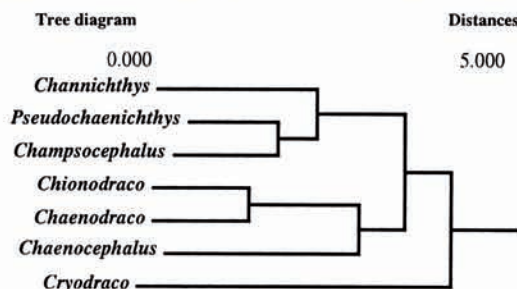
The cleithrum of all the channichthyids appears with the small anterior ascending process decreasing and disappearing later (Fig. 3A-C). The development of the pectoral girdle is the same as in the other notothenioids (Voskoboinikova and Tereshchuk, 1991; Voskoboinikova *et al.*, 1994). Previously, four free radials appear, the dorsal of which fusing later with the scapula (Fig. 3A-D). Among the channichthyids, adults of *Channichthys* are characterized by a position of the scapular foramen in the upper part of the coracoid as in some other more primitive notothenioids (Iwami, 1985). Iwami considered this character of *Channichthys* as apomorphic. In larvae and juveniles of *Channichthys* the coracoid is developing much faster than in other species of channichthyids. This is a reason why the coracoid in adults of *Channichthys* has a full development, while other channichthyids are characterized by a reduction of this bone. So, the structure of the coracoid of *Channichthys* should be considered as plesiomorphic.

The development of the caudal skeleton of the channichthyids is similar to the development of the caudal skeleton of the nototheniid *Pleuragramma antarcticum* (Totton, 1914; Voskoboinikova *et al.*, 1994) and of the bathydraconid *Psilodraco*. Previously the hypaxial lobe is formed by the two hypurals h1 and h2 which later fuse between each other (Fig. 3F). In the epaxial lobe, the appearance of the hypural 3 (Fig. 3F) is followed by the hypural 4 (Fig. 3G) which also fuse later with the hypural 3 (Fig. 3H) and with the urostyle in the adults. In some species, e.g. *C. gunnari*, two urostylar centra are present but later fuse between each other.

Rate of the osteological development

Previous investigation of the osteological development of the nototheniids showed that it is possible to speak about the rate of development based on the appearance of the different bony elements in ontogenesis (Voskoboinikova, 1994). The rate of the osteological development of channichthyids is slower than the rate of development of the nototheniids (Voskoboinikova, 1994) and bathydraconids, that could be the manifestation of the pedomorph character of evolution in the suborder Notothenioidei; this was already noted in nototheniids (Balushkin, 1984; Voskoboinikova, 1994), bathydraconids and channichthyids (Iwami, 1994). Among the channichthyids, late appearance of bony elements is also pronounced (Table I). Three groups of genera are revealed on the basis of the rate of the osteological development (data on 54 bones were available in all genera, except *Pagetopsis*) (Table II). The first of them includes *Champscephalus*, *Pseudochaenichthys* and *Channichthys*, the latter showing some late appearance of bo-

Table II. - Diagram of the genera of channichthyids based on the appearance of bones during ontogenesis. Metric distance is euclidean distance using the Ward minimum variance method.



nes. I had not enough material on the development of *Pagetopsis*, but on the basis of available material (Table I), it seems possible to place it also in the first group. *Pagetopsis* also shows an appearance of most of the bones later than for *Champscephalus* and *Pseudochaenichthys*. The second group includes *Chionodraco*, *Chaenodraco* and *Chaenoccephalus* among which *Chaenoccephalus* shows a late appearance of the bones. The third group is formed by *Cryodraco* which has the latest appearance of the skeletal elements. The phenogram shows the obvious delay in the osteological development of the channichthyids from the first to the third group. Therefore, it is possible to speak about a paedomorph character of the evolution into the family Channichthyidae, based on the osteological development.

DISCUSSION

The study of the osteological development of eight species of the family Channichthyidae shows that the channichthyids are very homogeneous concerning the sequence of appearance and morphogenesis of the skeletal elements. Most differences between genera of the channichthyids were revealed in the rate of the osteological development. It is possible to divide the channichthyids in three groups according to the rate of appearance of most of the bony elements. The two first groups correspond to the groups proposed by Regan (1914) and Balushkin (1996) from the analysis of the data available on morphological and axial skeleton. The unusual position of *Cryodraco* can be explained by a very late appearance of the bones in that genus. In general, a late osteological development of the channichthyids, compared to the nototheniids and bathydraconids, can be related to a paedomorph evolution of the channichthyids within the suborder Notothenioidei. Iwami (1994) noted the paedomorph character of the evolution in two groups of channichthyids on the basis of the adult osteological characters: the *Pagetopsis*-group including the genera *Pagetopsis*, *Pseudochaenichthys* and *Neopagetopsis* among which *Pagetopsis* shows some progenetic character states, and the *Chaenoccephalus*-group including the genera *Chaenoccephalus*, *Cryodraco* and *Chionobathyscus*, among which *Cryodraco* has some neotenic condition. Based on circumstantial evidences, Iwami (1994) concluded that paedomorphosis is one of the most important process of speciation of the channichthyids. So the data on the osteological development support the point of view of Iwami on the role of paedomorphosis in the evolution of the channichthyids.

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